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Published in:
Marine Ecology - Progress Series

Link to article, DOI:
[10.3354/meps175129](https://doi.org/10.3354/meps175129)

Publication date:
1998

Document Version
Publisher's PDF, also known as Version of record

[Link back to DTU Orbit](#)

Citation (APA):
Viitasalo, M., Kiørboe, T., Flinkman, J., Pedersen, L. W., & Visser, A. (1998). Predation vulnerability of planktonic copepods: consequences of predator foraging strategies and prey sensory abilities. *Marine Ecology - Progress Series*, 175, 129-142. <https://doi.org/10.3354/meps175129>

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Predation vulnerability of planktonic copepods: consequences of predator foraging strategies and prey sensory abilities

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ABSTRACT: We investigated the vulnerability of 2 copepod species (*Eurytemora affinis* and *Temora longicornis*) to predation by predators with different foraging modes, three-spined stickleback *Gasterosteus aculeatus* juveniles and mysid shrimps *Neomysis integer*. Copepods were videofilmed escaping from predators and from an artificial flow field, and the results were used in a model of hydrodynamic disturbance generated by a predator. The copepods detected mysids from a significantly larger distance than they detected sticklebacks (0.45 and 0.24 cm, respectively). Consequently, the capture success of the sticklebacks was higher than that of mysids. In the case of sticklebacks foraging on *E. affinis*, copepod reaction distance was significantly correlated with stickleback approaching speed; sticklebacks captured a copepod only if they were able to slowly approach to within a strike distance of <0.1 cm from the prey. Also, there was a major difference between the vulnerabilities of the 2 prey species: the capture success of sticklebacks was 92% with *T. longicornis* and 53% with *E. affinis*. This corresponded with experiments with artificial flow, where the threshold fluid velocity gradient eliciting an escape response in copepods was 4 times higher in *T. longicornis* than in *E. affinis* (8.2 and 2.1 s⁻¹, respectively). The hydrodynamic model accurately predicted the positive relationship between stickleback approaching speed and copepod reaction distance, as well as the difference between the 2 copepod species. This suggests that, by using simple artificial flow experiments, we can rank various zooplankton species according to their escape capabilities, and thus predict their vulnerability to predation by small fish with different motility patterns. In contrast, the model did not conform with observations on mysids. Apparently, the hydrodynamic disturbance created by a mysid is not related to its swimming speed, but to some other factor, such as the beat rate of swimming appendages.

KEY WORDS: Predation vulnerability · Escape response · Hydrodynamic signals · Prey selection · *Eurytemora affinis* · *Temora longicornis* · *Gasterosteus aculeatus* · *Neomysis integer*

INTRODUCTION

The vulnerability of a planktonic prey to predation can be measured as the product of the encounter rate with predator and the escape success of the prey (Pas-

torok 1981, Greene 1986). The encounter rate is directly proportional to the velocity difference between predator and prey (Gerritsen & Strickler 1977, Tiselius et al. 1993) as well as prey characteristics that affect the predator's reactive distance, such as prey size (Brooks & Dodson 1965, Gardner 1981, Flinkman et al. 1992), colour contrast (Zaret 1972, Zaret & Kerfoot 1975, Buskey 1994) and behaviour (O'Brien et al. 1976, Williamson 1980, Zaret 1980, Yen & Strickler 1996). The escape success, in contrast, depends on the

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perceptive ability of the prey and its behavioural and morphological defences.

Both planktonic predators and prey can be classified into functional groups according to their swimming and feeding behaviour. These behaviours significantly influence the outcome of the predatory interaction, through their effect on encounter rates and prey escape capabilities. For instance, predators may search for prey by 'cruising' or 'ambushing'. Cruising predators locate prey by fast swimming, while predators that ambush mainly rely on prey movement (or water motion) in encountering prey. Because many planktonic prey species use mechanosensing in detecting predators (e.g. Strickler & Bal 1973, Strickler 1975), and because cruising creates a larger hydrodynamic signal than ambushing, there is a trade-off between optimisation of encounter rates and maximisation of capture success. Predators therefore often use intermediate stop-and-go search patterns (O'Brien et al. 1989, 1990) and vary their swimming behaviour according to prey availability (Coughlin et al. 1992). Also, the perceptive ability of prey is intimately linked to their behavioural ecology. In particular, copepods have mechanosensing hairs and setae on their body and antenna, which are especially conspicuous in species that hunt for motile prey, such as ciliates or copepod nauplii (Fleminger 1973, Strickler & Bal 1973, Strickler 1975, Yen et al. 1992). It is therefore possible that predatory copepods are better able to detect hydrodynamic disturbance created by their own predators than predominantly suspension feeding copepods.

The escape performance of different zooplankton taxa has been investigated by subjecting the experimental animals to flow fields created by pipettes or moving obstacles (e.g. Szlauer 1964, 1965, Singarajah 1969, 1975, Janssen 1976, Drenner et al. 1978, Landry 1978, Drenner & McComas 1980). Later videographic studies have also quantified the flow fields around predators and prey. However, most of the detailed videographic studies have experimented with artificial (Haury et al. 1980, Gilbert & Kirk 1988, Kirk & Gilbert 1988, Buskey 1994, Fields & Yen 1996) or tethered predators (Drost 1987, Yen & Fields 1992) and with small rotifer and cladoceran prey that possess limited escape capabilities. In studies where interactions between larger zooplankton and free-swimming predators have been analysed in detail (e.g. Drost 1987, Drost et al. 1988, Kils 1992), the spatial scales and the viewpoint of the study have essentially been those of the predator.

We investigated the escape and sensory capabilities of 2 copepod species, *Eurytemora affinis* and *Temora longicornis*, when preyed upon by 2 different predators, three-spined stickleback *Gasterosteus aculeatus*

juveniles and mysid shrimps *Neomysis integer*. These 4 experimental species represent different functional predator and prey groups: three-spined sticklebacks are visual predators that search for prey in a stop-and-go fashion (Beukema 1968), whereas mysid shrimps are usually held non-visual cruisers that prey on small prey by creating a feeding current and on larger prey by raptorial feeding (Cooper & Goldman 1980, Mauchline 1980, Siegfried & Kopache 1980, Grossnickle 1982). There is a major difference in the swimming modes of the predators as well: sticklebacks mainly swim by thrusts of the tail, whereas mysids propel themselves forward by paddling with their thoracic appendages. This probably makes the hydrodynamic disturbance produced by mysids and sticklebacks very different. Our objectives were to compare the susceptibilities of the 2 copepod species to predation by these predator types, and to determine how well simple hydrodynamic laws explain the observed responses. This was accomplished by videofilming copepods escaping from the predators and from an artificial flow field, and by combining the information into a simple model of hydrodynamic disturbance generated by a predator.

MATERIALS AND METHODS

Experimental organisms and sampling. *Eurytemora affinis* (Poppe) and *Temora longicornis* (Müller) are common calanoid copepod species in the Baltic Sea. Both species are as adults ~1 mm long; *E. affinis* females carry the eggs in an egg sac, while *T. longicornis* sheds its eggs freely in the water. In the Baltic Sea, both species are important prey for various planktivores, such as clupeids (Sandström 1980, Flinkman et al. 1992, 1998), sticklebacks (Hangelin & Vuorinen 1988, Leinikki 1995) and mysid shrimps (*Mysis* spp.) (Hansson et al. 1990, Rudstam et al. 1992, Mohammadian et al. 1997, Viitasalo & Rautio 1998). Three-spined sticklebacks *Gasterosteus aculeatus* L. occur both in the sublittoral and in the open sea, and feed mainly on crustacean zooplankton (Beukema 1968, Rajasilta 1980, Thorman & Wiederholm 1986, Leinikki 1995). *Neomysis integer* (Leach) usually dwells in relatively shallow water and feeds on a large variety of planktonic and benthic food items, including copepods (Irvine et al. 1993, Uitto et al. 1995, Nordström 1997).

The experimental animals were collected in August 1996 ('predator experiments') and in August 1997 ('experiments with artificial flow') in the archipelago of Hanko Peninsula, SW Finland. The copepods were collected with a Hensen plankton net (mesh size 100 µm), from 0 to 20 m depth. The sample was poured into a cool box with 15 l of seawater from ca 0, 20 and 30 m

depth (5 l from each depth). The cool box was quickly taken to a temperature controlled room (15°C in 1996 and 13°C in 1997), and the water was aerated. Copepods were picked from the sample and placed into 1 l glass jars with filtered seawater with aeration. Predators were collected the same day from a nearby sublittoral area by using small nets and an epibenthic sledge-sampler. The fish and mysids were taken into the laboratory, measured and placed in 2 l glass jars containing filtered seawater. Aeration was begun and the animals were left to acclimate to laboratory conditions for ca 2 d.

Filming equipment. The animals were filmed in 1 l cubic Plexiglas aquaria. Illumination for the cameras was provided by infrared light emitting diodes (LEDs). To enable measurements of distances and velocities in 3 dimensions, 2 video cameras (Mintron MTV-1802CD equipped with 35 mm Nikkor lenses) were fixed at right angles at 90 cm distance from the aquarium. The 2 images were combined onto 1 monitor with an image mixer, and recorded with a Panasonic VCR (resolution 50 frames s⁻¹). Time in $\frac{1}{100}$ s was displayed on the monitor with a video timer. In the predator experiments the area seen on the monitor was 8 cm wide and 8 cm high, and the depth of field covered the whole aquarium; in the experiments with artificial flow, the view was 4 cm wide and 6 cm high. A third camera (with a 105 mm macro lens) was placed on a tripod to obtain 2-dimensional close-up views. The magnification in the close-ups varied according to position of the objects in the aquaria and turning and moving of the tripod. We hereafter refer to films made with the 2 cameras and at low magnification as '3-D films', while the films made with 1 camera and at high magnification are called 'close-up films'.

Predator experiments. The experiments with sticklebacks were made in room light, whereas the experiments with mysids were performed in darkness (except for the infrared LEDs). However, when making the close-up films, the monitor was on, which created a low light in the room.

In the first experiment (Expt 1), 3 *Neomysis integer* (each 1.0 cm in length) were placed in an aquarium with 40- μ m-filtered seawater and 80 egg-carrying *Eurytemora affinis* females, and the interactions were filmed at high and low magnifications. In the second experiment (Expt 2A), 3 stickleback juveniles (lengths 1.5, 1.7 and 1.8 cm) were placed in an aquarium with 40- μ m-filtered seawater and 130 egg-carrying *E. affinis* females. The fish ate the prey rapidly, so ~200 additional copepods were picked and given to the fish (Expt 2B).

Experiments with *Temora longicornis* were made the next day (Expt 3). First, 70 adult *T. longicornis* females were transferred into the aquarium with the same *Neomysis integer* as in Expt 1 (which had been kept

overnight in the aquarium without food). Second, *T. longicornis* were filmed with sticklebacks. Because *N. integer* managed to capture only very few prey, the *T. longicornis* from the Expt 3 were given to the sticklebacks from the Expt 2 (which had been kept in a 2 l glass jar without food overnight) (Expt 4A). As the fish again rapidly depleted the prey, ~100 new *T. longicornis* were picked and given to the sticklebacks (Expt 4B).

Experiments with artificial flow. The experiments with artificial flow were conducted in dim room light, in similar 1 l aquaria as in the predator experiments. A Pasteur pipette was fixed vertically (from above) into the middle of the aquarium and connected to a thin silicon tube with its free end hanging below the aquarium; this created a water flow to which the copepods reacted. To be able to quantify the flow field, a small amount of cultured phytoplankton was added into the aquarium. Then, 100 *Eurytemora affinis* were added and the escape reactions were filmed as above. When the water level was close to the tip of the pipette, more water was added, and filming was continued until a sufficient number of escapes and captures were observed. The same procedure was repeated with 100 *Temora longicornis*. With this set-up, the hydraulic head height increased by ~10% during each fill, but, since flow in the outlet tube was turbulent, volume flow scales with the square-root of the head height. Thus, the volume flow varied by only ~5% during each fill. We restricted our analysis to the region in front of (i.e. below) the pipette.

Analyses of video films. Time and distance measurements of the predatory interactions were made with an image analysing program. We defined an 'interaction' as starting when a predator detected a prey (or when a prey detected a predator) and ending when the predator captured or lost the prey. One interaction may thus contain several escapes, attacks and pursuits. In the case of sticklebacks, prey detection was distinguished from a sharp turn by which the fish oriented towards the prey. The interactions with mysids were identified from a combination of a copepod escape response and a sharp movement by the mysid. Each interaction was analysed frame by frame. Positions of the prey and the nose or rostrum of the predator were marked on the 2 perpendicular views, which resulted in x-y-z and time coordinates. From these records we calculated prey location and attack distances of predators, reaction distances of copepods to predators, as well as velocities for fish, mysids and copepods during various sequences of the interactions (Table 1). All interactions that took place closer than ~1 cm from aquarium walls were excluded from the analysis. The foraging success of fish and mysids was assessed from the 3-D films as the fraction of interactions ending with capture. The

Table 1. Terms used in the text and parameters recorded from the films

Variable	Definition
Interaction	Encounter between a predator and a prey that starts with location of the prey and ends with prey being captured or escaping outside the visual or sensory field of the predator. One interaction may contain several attacks, escapes and pursuits
Predator	
Prey detection distance	Distance from which the predator detects the prey. For example, a stickleback sharply turns towards a copepod and initiates approach or a mysid clearly reacts to a copepod
Approach	For sticklebacks, the sequence between detecting the prey and initiating attack; for mysids, the period when swimming towards the copepod
Approach speed	Speed during an approach; in the case of sticklebacks, calculated for the period when the fish are within 0.5 cm of the copepod; in the case of mysids, calculated for the last ~0.4 s of the approach
Attack distance	Distance between the nose/rostrum of the predator and the copepod at the beginning of the attack
Attack speed	Speed of the predator during the first 0.06 s of the attack
Pursuit	A sequence where the prey escapes but remains in the visual or sensory field of the predator, which starts a new approach
Prey	
Reaction distance	Distance between the copepod and nose/rostrum of the predator at the beginning of escape
Escape speed	Speed of the copepod during the first 0.06 s of the escape
Total escape distance	Total distance travelled by the copepod during the escape, until it stopped completely
Escape duration	Total duration of the escape, until it stopped completely

close-up films were mainly made to obtain qualitative information, but some measurements concerning mysid attack speeds were also made from them. This was done by measuring jump distances from the screen, and by scaling the measured distances with the mysid body length (1 cm).

In the experiments with artificial flow, the 3-dimensional flow field was quantified by analysing the velocities of 78 neutrally buoyant particles approaching the opening of the pipette (altogether 419 velocity-location data points). Copepod reaction distances from the mouth of the pipette were then measured. In cases where copepods performed several sequential escape jumps, only the first one was measured.

The hydrodynamic model. A predator moving through water generates velocity gradients in the ambient fluid, which copepods are believed to be able to perceive (Yen & Fields 1992, Fields & Yen 1996, Yen & Strickler 1996). Copepods have hairs and setae on their body and antenna, and it is assumed that it is the bending of these setae that the copepods sense (Strickler & Bal 1973, Gill 1985, Yen et al. 1992, Fields & Yen 1996, 1997). Such bending may occur if there is a velocity difference between the copepod and the ambient fluid. The magnitude of the hydrodynamic signal potentially produced by the predator may, in the case of the approaching fish, be analysed by a simple model.

Following Tiselius & Jonsson (1990), we can examine the velocity gradients generated by the fish by modelling the approaching fish as a translating sphere with a

diameter equal to the diameter of the (front part) of the fish, and by assuming streamlines following creeping flow solutions (Berg 1993). This is a great simplification but may be warranted by the fact that, after having located the prey, the fish pushes itself forward by means of a thrust of the tail and approaches the prey front on. The radial and azimuthal components of the velocity of the fluid (v_r and v_θ , respectively) relative to the sphere are (Berg 1993):

$$v_r(r, \theta) = -U \cos \theta \left(1 - \frac{3a}{2r} + \frac{a^3}{2r^3} \right) \quad (1)$$

$$v_\theta(r, \theta) = U \sin \theta \left(1 - \frac{3a}{4r} - \frac{a^3}{4r^3} \right) \quad (2)$$

where U is the velocity of the sphere, a the radius of the sphere, r the radial distance from the centre of the sphere and θ the angle relative to the direction of motion of the sphere. The velocity gradients in this flow field can be decomposed into gradients along the streamlines and gradients perpendicular to the streamlines. The magnitude and distribution of these 2 components of the flow field are contoured in Fig. 1. In front of the approaching fish, velocity gradients along the streamlines (Fig. 1A) are at maximum and vary with the distance to the sphere, while the velocity gradients perpendicular to streamlines (Fig. 1B) are zero. For simplicity, and because the fish approaches the prey front on, we shall only consider fluid velocities directly in front of the sphere. At $\theta = 0$, the fluid veloc-

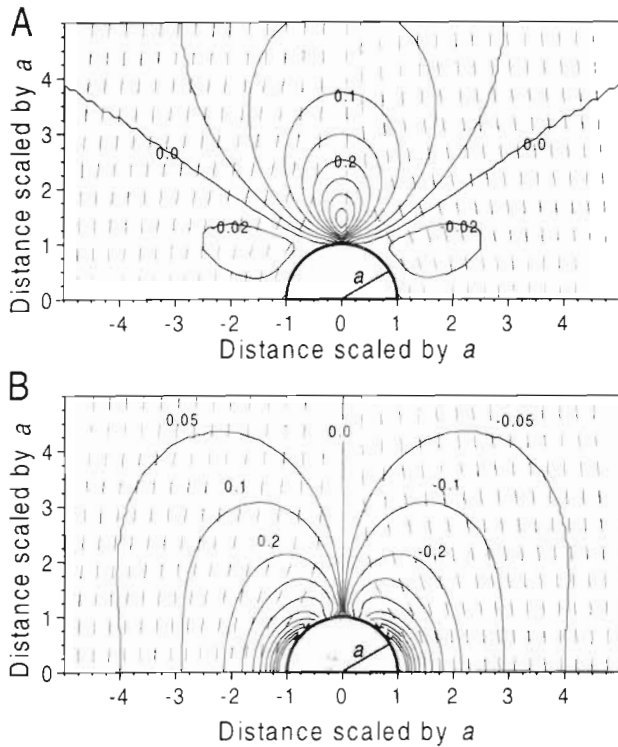


Fig. 1. Contour lines of the flow field produced by a translating sphere. The gradient in absolute velocity (A) in the along-streamline direction and (B) in the across-streamline direction. Streamlines are indicated by dashed lines. Velocity gradient units are scaled by U/a , where U is the velocity of the sphere and a is its radius

ity as a function of the distance to the sphere is given solely by Eq. (1), which thus simplifies to

$$v(r) = -U \left(1 - \frac{3a}{2r} + \frac{a^3}{2r^3} \right) \quad (3)$$

and the velocity gradient as a function of predator approach speed is

$$\frac{\partial v}{\partial r} = \frac{3Ua}{2r^4} (r^2 - a^2) \quad (4)$$

Assume now that the signal perceived by the copepod is directly proportional to the velocity gradient (as suggested below), and that there is a threshold velocity gradient, γ^* , that elicits an escape response in the copepod. By inserting this threshold gradient into the Eq. (4), the reaction distance, $R = r(\gamma^*) - a$, can be estimated as

$$R = a \sqrt{\frac{3U}{4a\gamma^*} \left(1 + \sqrt{1 - \frac{8a\gamma^*}{3U}} \right)} - a \quad (5)$$

The dotted lines in Fig. 2 illustrate how the copepod reaction distance R varies as a function of the approach velocity of the fish for $a = 0.1$ cm (the radius of the front

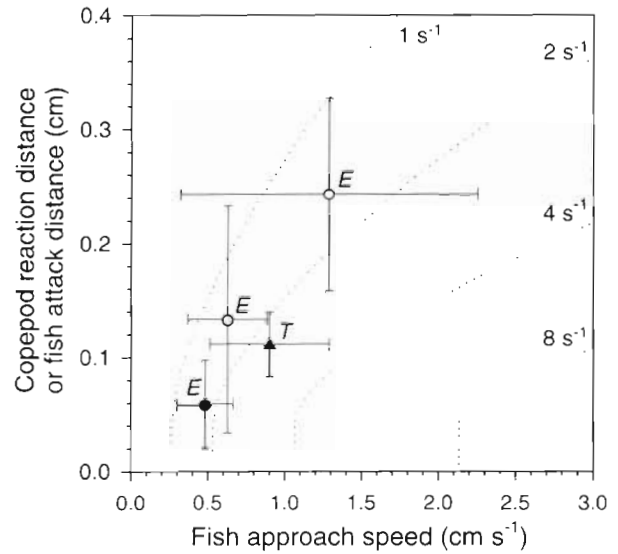


Fig. 2. Model of reaction distances of copepods as a function of predator (e.g. a stickleback with a nose radius, a , of 0.1 cm) approach velocity. The 4 dotted isolines denote predicted reaction distances at arbitrary threshold velocity gradients (1, 2, 4 and 8 s^{-1}) at which copepods react to a simulated suction by a pipette. Symbols denote observations from the predator experiment (copepods escaping from sticklebacks; see 'Results'). (●) *Eurytemora affinis* (E) captures; (○) *E. affinis* escapes during attack; (○) *E. affinis* escapes before attack; (▲) *Temora longicornis* (T) captures. Vertical and horizontal bars denote SD

part of the fish). The 4 isolines, for arbitrary threshold velocity gradients of 1, 2, 4 and 8 s^{-1} , show that lower threshold velocity gradients (i.e. higher prey sensitivities) and higher predator approach speeds elicit escape responses at longer distances. None of the combinations of approach speed and distance between predator and prey that lie above each isoline will elicit an escape, whereas combinations below the line should not exist, since at the isoline the copepod escapes and thus increases its distance from the predator. For a complete description of the model and the theory behind it, refer to Kjørboe & Visser (1999).

RESULTS

Outcome of interactions in predator experiments

We divided the predatory interactions between sticklebacks, mysids and the 2 copepod species into distinct components, i.e. search, prey detection, attack, capture/escape, and handling (Holling 1959, Gerritsen & Strickler 1977, Kerfoot 1978). Fig. 3 gives an example of the events that took place from prey detection to capture or escape, during the 137 interactions recorded between sticklebacks and *Eurytemora affi-*

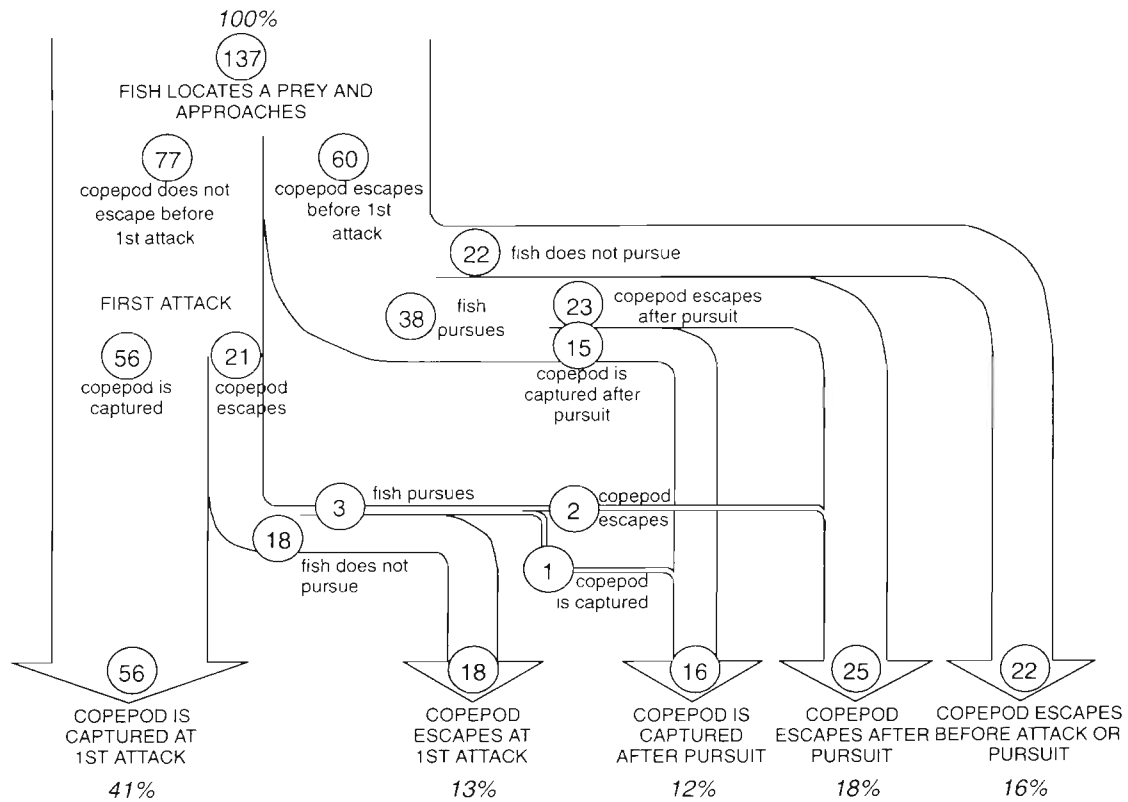


Fig. 3. *Gasterosteus aculeatus* vs *Eurytemora affinis*. Flow chart of the 137 predatory interactions in Expts 2A and 2B. Encircled numbers refer to the absolute number of interactions of each type; percentages are given as percentages of the total number of interactions

nis. The most profitable strategy for sticklebacks was to approach to within a strike distance and attack before the copepod detected the predator. Sticklebacks captured *E. affinis* at first attack in 41% of the cases and captured prey after pursuit in 12% of cases

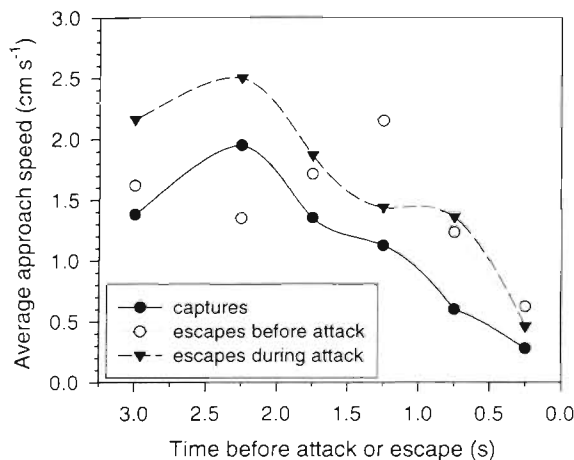


Fig. 4. *Gasterosteus aculeatus* vs *Eurytemora affinis*. Variations in the average approach speed of sticklebacks in cases where the prey was captured or escaped before or during the attack

(Fig. 3). The overall capture success of sticklebacks preying on *E. affinis* was thus 53%. The capture success after pursuit was relatively poor: if the copepod escaped before the first attack, the fish followed in 38 cases out of 60 but captured the prey only in 15 cases.

With *Temora longicornis*, none of the stickleback attacks seen on 3-D films failed and only in 1 interaction out of 12 did the copepod escape before attack. The overall capture success of sticklebacks with *T. longicornis* was thus 92%. In contrast, none of the *Neomysis integer* on the 3-D films succeeded in capturing either of the copepod species. However, we recorded a few captures on the close-up films (see below).

Predator approach strategies

When searching for a prey, the sticklebacks usually stayed in an almost fixed position, detecting prey from a mean distance of 2.06 to 2.25 cm (Table 2A). After locating a prey, the fish sharply accelerated but, when getting closer to the prey, it markedly slowed down (Fig. 4). The mean final approach speed of the fish (calculated for a range within 0.5 cm from the prey, which

Table 2. Predator experiment. (A) Predators' prey detection distances, (B) approach speeds, (C) attack distances and (D) attack speeds with the 2 prey species. n = no. of observations

Variable/prey	Predator	
	Stickleback Mean \pm SD (n)	Mysid Mean \pm SD (n)
(A) Prey detection distance (cm)		
<i>Eurytemora affinis</i>	2.25 \pm 1.00 (32)	0.92 \pm 0.01 (2) ^a
<i>Temora longicornis</i>	2.06 \pm 0.68 (10)	No data
(B) Approach speed (cm s⁻¹)		
<i>Eurytemora affinis</i>	0.96 \pm 0.82 (32)	3.02 \pm 0.97 (44)
<i>Temora longicornis</i>	1.07 \pm 0.37 (9)	0.96 \pm 0.37 (8)
(C) Attack distance (cm)		
<i>Eurytemora affinis</i>	0.08 \pm 0.06 (18)	~0.8 (1) ^b
<i>Temora longicornis</i>	0.11 \pm 0.03 (11)	No data
(D) Attack speed (cm s⁻¹)		
<i>Eurytemora affinis</i>	4.17 \pm 2.22 (17)	~53 (1) ^b
<i>Temora longicornis</i>	6.27 \pm 1.57 (11)	No data

^aMysid responded to a copepod escaping

^bMysid attack distance and speed estimated from a close-up film

corresponds to the maximum perceptive zone of the copepods; see below) was 0.96 cm s⁻¹ with *Eurytemora affinis* and 1.07 cm s⁻¹ with *Temora longicornis* (Table 2B). With *E. affinis*, the fish final approaching speed was significantly lower (Student's *t*-test value = 2.17, *p* = 0.038, *df* = 30) in cases when the prey was captured (mean approaching speed 0.48 cm s⁻¹) than when *E. affinis* escaped (mean approaching speed 1.14 cm s⁻¹)

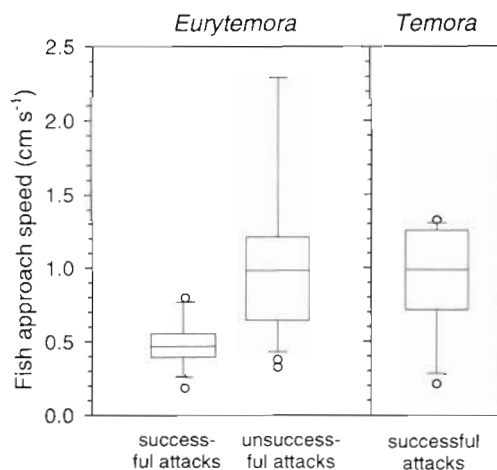


Fig. 5. *Gasterosteus aculeatus* vs *Eurytemora affinis* and *Temora longicornis*. Box plot of the mean final approach speed of sticklebacks (within 0.5 cm distance from the prey) preying on copepods. Middle horizontal line: median; lower and upper ends of box: 25th and 75th percentiles; and ends of whiskers: the 10th and 90th percentiles of the data. (O) Outliers outside the 10th and 90th percentiles. Difference between the *E. affinis* data sets is statistically significant (Student's *t*-test value = 2.17, *p* = 0.038)

(Fig. 5). A similar distinction could not be made for fish approaching *T. longicornis*: all approaches but one were successful, although the fish approached *T. longicornis* at a relatively high speed (Fig. 5).

The mysids were cruise predators, but they also spent a large part of their time on the bottom. The estimate of *Neomysis integer* 'prey detection' distance (0.92 cm; Table 2A) comes from 2 observations where *Eurytemora affinis* escaped before attack, which stimulated the mysid to jump. It is not certain if these jumps were capture attempts or escape reactions by the mysid. The mysids did not slow down when approaching a prey. Their mean approach speed with *E. affinis* (measured for the last 0.4 s before the copepod escape) was ca 3 times higher than that of sticklebacks (Table 2B). In the experiment with *Temora longicornis*, only 8 interactions were recorded. Mostly only 1 mysid swam freely, at slow speed (0.96 cm s⁻¹); others remained on the bottom of the aquarium.

Predator attack behaviour

Very close to the prey the sticklebacks froze in a typical attack position, with the tail slightly curved. The attack distance was on average 0.08 cm with *Eurytemora affinis* and somewhat longer with *Temora longicornis* (0.11 cm) (Table 2C). The sticklebacks made successful attacks on *E. affinis* from a mean distance of 0.06 cm, whereas all attacks from 0.15 to 0.25 cm distance were unsuccessful (Fig. 6). No attacks were initiated from >0.25 cm distance. The average attack speed was 4.17 and 6.27 cm s⁻¹ with *E. affinis* and *T. longicornis*, respectively (Table 2D). *T. longicornis* were easier prey than *E. affinis*: the sticklebacks approached and attacked, and made a successful capture with seemingly little effort. We observed no escape attempts by *T. longicornis* at the moment of attack.

When a *Neomysis integer* cruised towards a copepod, the copepod detected the mysid before attack and was never captured. However, we made a few noteworthy observations on the close-up films. In one sequence, a mysid sitting on the bottom darted towards an *Eurytemora affinis* at a speed of ~53 cm s⁻¹. This sequence proved that *N. integer* sometimes uses an ambush mode and is able to move faster than a copepod (with mean escape speeds of ~7 to 13 cm s⁻¹, see below). Another sequence revealed that *N. integer* may pursue an escaped prey. *N. integer* attacked an *E. affinis*, which escaped but remained, apparently injured, on the bottom at about 1 cm distance from the mysid. The mysid started to move in ~2 cm wide circles, hitting and attacking the copepod unsuccessfully 4 times before it—29 s after the first attack—managed to grab the prey. Handling of the prey lasted for 1 min 56 s.

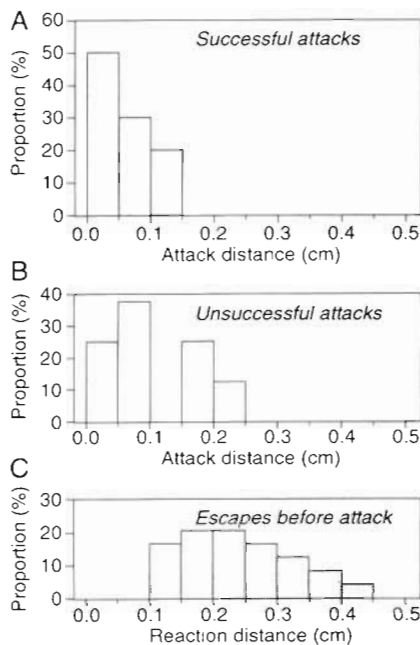


Fig. 6. *Gasterosteus aculeatus* vs *Eurytemora affinis*. Frequency distribution of fish attack distances (A) when prey was captured and (B) when prey escaped; (C) *E. affinis* reaction distances. Data from Expts 2A and 2B

Copepod escape behaviour

Eurytemora affinis reacted to an approaching stickleback from a mean distance of 0.24 cm (Table 3A) (maximum 0.40 cm). *E. affinis* were thus able to detect the fish 0.1 to 0.3 cm outside the potential attack range of the fish (cf. Fig. 6). The mean escape speed of *E. affinis* (8.58 cm s^{-1} ; Table 3B) was twice as high as stickleback attack speed (cf. Table 2D). In contrast, the escape speed of *Temora longicornis* (mean 7.05 cm s^{-1} ; Table 3B) was not significantly higher than the attack speed of sticklebacks.

Table 3. Predator experiment. (A) Copepods' reaction distances (in escapes before attack) and (B) escape speeds, with different predators (in escapes before or during attack). n = no. of observations

Variable/predator	Copepod species	
	<i>Eurytemora affinis</i> Mean \pm SD (n)	<i>Temora longicornis</i> Mean \pm SD (n)
(A) Reaction distance (cm)		
Stickleback	0.24 ± 0.08 (24)	0.22 (1)
Mysid	0.45 ± 0.13 (44)	0.33 ± 0.10 (8)
(B) Escape speed (cm s^{-1})		
Stickleback	8.58 ± 4.31 (32)	7.05 (1)
Mysid	12.79 ± 4.23 (44)	6.82 ± 2.02 (8)

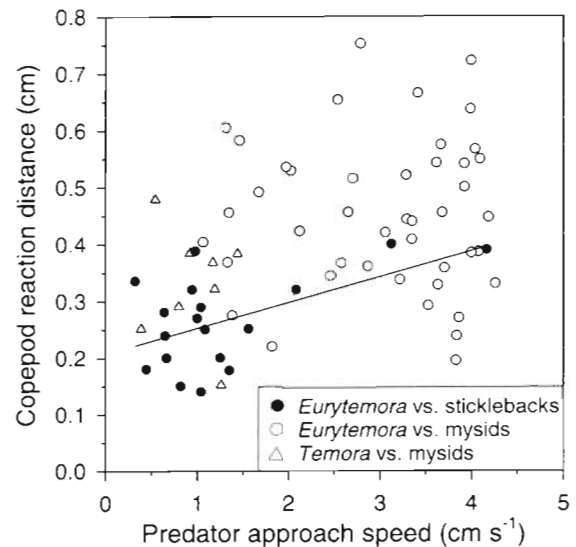


Fig. 7. *Gasterosteus aculeatus* and *Neomysis integer* vs *Eurytemora affinis* and *Temora longicornis*. Copepod reaction distances as a function of predator approach speed. Line: linear regression through stickleback-*E. affinis* data ($r^2 = 0.29$, F -ratio = 6.374, $p = 0.023$)

Eurytemora affinis reacted to mysids from a significantly longer distance than to sticklebacks (means 0.45 and 0.24 cm, respectively; Table 3A) (Student's t -test value = 6.99, $p < 0.0001$, $df = 66$). Also, the escape speed of *E. affinis* was higher when escaping from mysids than when evading fish (12.79 vs 8.59 cm s^{-1} ; Table 3B). *Temora longicornis* did not react differently to the predators.

When escaping before a stickleback attacked, *Eurytemora affinis* performed short (mean length 0.81 cm) sequential escapes, with the fish pursuing for up to 10 s. When escaping during attack, *E. affinis* travelled a longer distance (mean 1.81 cm, max. 5.85 cm), and often used an irregularly shaped, zigzagging or spiralling path. This apparently confused the sticklebacks, because they were rarely able to relocate the escaped *E. affinis*. In contrast, *Temora longicornis* performed simpler, forward-darting escapes.

The reaction distance of *Eurytemora affinis* was positively correlated with stickleback approach speed (Fig. 7, black circles; Pearson $r = 0.53$, $p = 0.023$, $n = 18$), but not with the approach speed of mysids (Fig. 7, open circles; Pearson $r < 0.001$, $p = 0.999$, $n = 44$). The observations on the *Temora longicornis*-mysid interaction did not show a consistent pattern (Fig. 7, grey triangles; Pearson $r = -0.139$, $p = 0.743$, $n = 8$). On the other hand, the approach speed of mysids (Fig. 8) was positively correlated with copepod escape speed (*E. affinis*: Pearson $r = 0.43$, $p = 0.004$, $n = 44$; *T. longicornis*: Pearson $r = 0.67$, $p = 0.069$, $n = 8$).

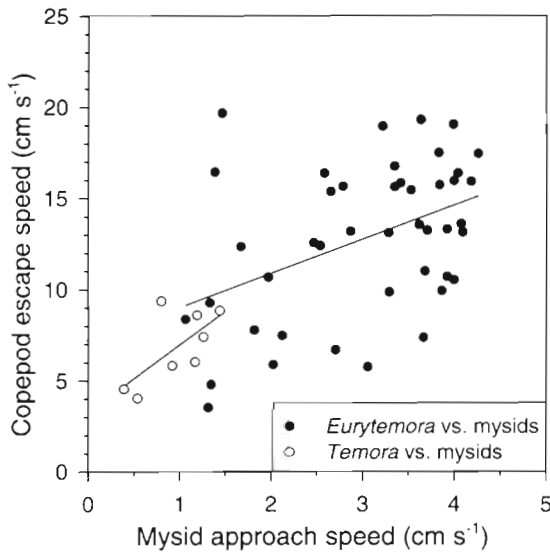


Fig. 8. *Neomysis integer* vs *Eurytemora affinis* and *Temora longicornis*. Escape speeds of *E. affinis* (●) and *T. longicornis* (○), as a function of approach speed of mysids. Solid lines: linear regressions through the 2 data sets (*E. affinis*: $r^2 = 0.18$, F -ratio = 9.397, $p = 0.004$; *T. longicornis*: $r^2 = 0.45$, F -ratio = 4.895, $p = 0.069$)

Experiments with artificial flow

In the experiment with artificial flow, *Eurytemora affinis* were never captured when they were drawn towards the pipette for the first time. In 5 cases the copepods were, however, captured after a long series of jumps against the flow. Thus, 9% of the 56 interactions ended in a 'capture'. In contrast, the 'capture success' with *Temora longicornis* was 74%: in 23 cases out of 50 were *T. longicornis* sucked into the pipette without escape, whereas 14 interactions ended in capture after 1 or more escapes.

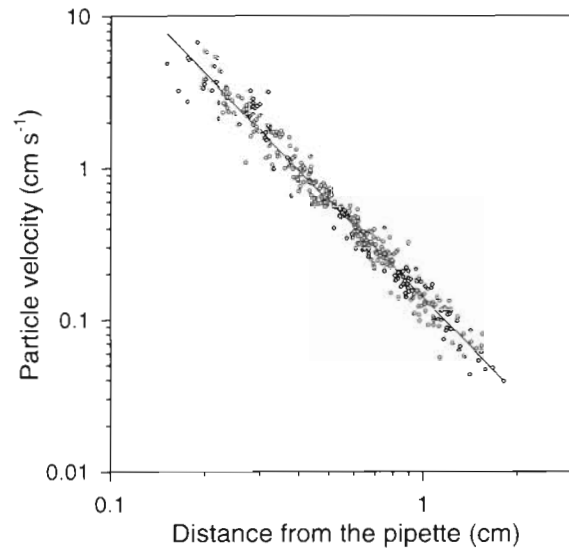


Fig. 9. Experiment with artificial flow. Velocities (v) of neutrally buoyant particles in relation to distance (r) from the opening of the pipette. Regression equation of the line is $v = 0.139r^{-2.125}$; variation explained, $r^2 = 0.97$

Fig. 9 shows the relationship between fluid velocity (v) and distance from the opening of the pipette (r), determined by following the near-neutrally buoyant particles. This relationship was described by $v = 0.139r^{-2.125}$ (variation explained, $r^2 = 0.97$). Fig. 10 shows the escape locations of *Eurytemora affinis* and *Temora longicornis* in this flow field. Note that in this presentation the third dimension (second horizontal axis, y) was removed by folding all escape points onto the x - z plane. The problem with this method is that it emphasises the number of observations farther away from the axis of the pipette, because they are integrated from a larger volume of water than those close to the axis of the pipette. However, this presentation

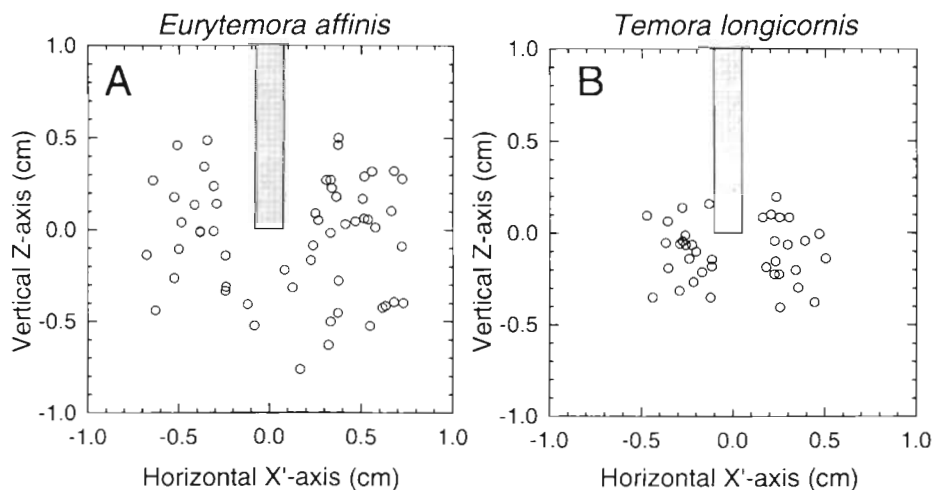


Fig. 10. Experiment with artificial flow. Escape locations of (A) *Eurytemora affinis* and (B) *Temora longicornis* relative to the pipette. The pipette is denoted by the shaded box; the opening of the pipette is at the origin of the coordinates. Note that the third dimension (second horizontal axis, y) has been removed by folding all escape points to the x - z plane (see text for further discussion)

Table 4. Experiment with artificial flow. Copepod reaction distances from the tip of the pipette and escape speeds during the first 0.06 s of the escape. Data include observations from below the level of the pipette opening. n = no. of observations

Variable	Copepod species	
	<i>Eurytemora affinis</i>	<i>Temora longicornis</i>
	Mean \pm SD (n)	Mean \pm SD (n)
Reaction distance (cm)	0.53 \pm 0.20 (28)	0.35 \pm 0.11 (29)
Escape speed (cm s ⁻¹)	5.51 \pm 2.51 (28)	4.69 \pm 1.75 (29)

correctly illustrates copepod reaction distances relative to the opening of the pipette. We note that *E. affinis* reacted to the pipette from a significantly larger distance than *T. longicornis* (means 0.53 cm and 0.35 cm, respectively; Table 4) (Student's *t*-test value = 4.49, *p* < 0.0001, df = 55).

Because the flow velocity increases approximately with distance to the pipette squared (cf. Fig. 9), a relatively small difference between the reaction distances of copepods implies a large difference between their hydrodynamic sensitivities. We can estimate the threshold flow velocities and velocity gradients that elicit an escape in the copepods by inserting the observed mean reaction distances (*r*) into the velocity equation, $v = 0.139 r^{-2.125}$, and into the velocity gradient equation, $\partial v / \partial r = 0.296 r^{-3.125}$ (obtained by differentiation of the velocity equation). Table 5 shows these thresholds calculated for the 2 copepod species. We note that, although the reaction distance of *Temora longicornis* was only 34% shorter than that of *E. affinis*, the average fluid velocity gradient that is needed to elicit an escape is 4 times higher in *T. longicornis* than in *E. affinis* (8.2 and 2.1 s⁻¹, respectively).

Table 5. Experiment with artificial flow. Reaction distances, *r* (cm), and estimates of thresholds for velocity, *v* (cm s⁻¹), and for velocity gradient, $\partial v / \partial r$ (s⁻¹), that elicit an escape response in *Eurytemora affinis* and *Temora longicornis* (calculated for the average reaction distance, *r*, and for *r* \pm standard deviation, SD)

Reaction distance	<i>v</i>	$\partial v / \partial r$
<i>Eurytemora affinis</i>		
<i>r</i> - SD = 0.33	1.41	8.89
<i>r</i> = 0.53	0.53	2.12
<i>r</i> + SD = 0.73	0.27	0.80
<i>Temora longicornis</i>		
<i>r</i> - SD = 0.24	2.96	26.51
<i>r</i> = 0.35	1.33	8.21
<i>r</i> + SD = 0.46	0.75	3.51

DISCUSSION

Our experiments showed that (1) the 2 copepod species had different susceptibilities to predation; (2) the reaction distance of one of the copepods (*Eurytemora affinis*) correlated with stickleback approach speed; and, consequently, (3) the capture success of the slow-approaching fish was higher than that of fish that approached their prey at a high speed. Furthermore, (4) both copepod species detected the mysids from a larger distance than they detected the sticklebacks, but (5) copepod reaction distance was not correlated with mysid approach speed. Below, we consider these findings in relation to hydromechanical signals generated by the predator and sensory abilities of the prey, and with respect to their behavioural modes.

Hydrodynamic considerations

The flow field created by the pipette resembles that directly in front of the approaching fish, in the sense that it is characterised solely by along-streamline velocity gradients. We therefore used the artificial flow to evaluate the magnitude of the threshold velocity gradient for the 2 copepod species. Ideally, the flow field generated by the pipette is characterised by velocity gradients that vary as a function of the distance to the pipette, while tangential velocity gradients are zero (see below, however). By noting the distance from the pipette at which the copepods escaped, threshold velocity gradients, γ^* , of ca 2 and 8 s⁻¹ were estimated for *Eurytemora affinis* and *Temora longicornis*, respectively (Table 5). The estimated isolines of copepod reaction distance versus fish approach speed with these threshold sensitivities were depicted in Fig. 2. If we now plot the reaction and attack distances observed in the predator experiments as a function of fish approach speed, we note that the mean observations compare favourably with the model, albeit with large variation (cf. the symbols and SD bars in Fig. 2). For instance, the higher threshold gradient estimated for *T. longicornis* is consistent with the almost entire lack of escape responses observed with sticklebacks: the combination of mean approach speed (0.90 cm s⁻¹) and attack distance (0.11 cm) in the successful attacks, and threshold gradient of 8.2 s⁻¹ (Fig. 2, filled triangle) would suggest that all approaches are successful, as observed (with one exception). Likewise, the combination of the mean attack distance (0.08 cm) and threshold velocity gradient (2.1 s⁻¹) for the stickleback-*E. affinis* combination would suggest that the fish should approach the copepod with a speed of <0.53 cm s⁻¹ in order not to be perceived. This agrees with the average approach speed of successful attacks observed,

0.48 cm s⁻¹ (cf. Fig. 5). And, finally, the combination of mean approach speed in the interactions where the fish were perceived before attack (1.29 cm s⁻¹) and a threshold gradient of 2.1 s⁻¹ for the stickleback-*E. affinis* combination predicts a reaction distance (*R*) of 0.18 cm for *E. affinis*. This is slightly less than actually observed (0.24 cm), but, due to the variability in the estimates of the threshold gradient, this is well within the standard error (0.8 to 8.9 s⁻¹) of the mean value estimated for *E. affinis* (cf. Table 5).

As noted above, we assume that the copepod perceives a hydrodynamic disturbance by the bending of extending setae. Such bending may occur if there is a velocity difference between the copepod and the ambient fluid. A velocity difference may occur by 2 mechanisms, one being proportional to acceleration of the fluid and the other being proportional to the velocity gradient. The first mechanism derives from the fact that a copepod has a density slightly higher than that of the ambient water. Its acceleration will therefore be somewhat less than that of the fluid. For a constant acceleration, the slip velocity (Δw_1) due to this mechanism is simply $\Delta w_1 = w_s a_f / a_g$, where w_s is the sinking velocity of the copepod, a_f the acceleration of the fluid ($= v \cdot \partial v / \partial r$), and a_g the gravitational acceleration. Therefore, the strength of the signal generated by this mechanism is directly proportional to the acceleration of the fluid. The second mechanism is due to the fact that copepods have spatial dimensions. Within a velocity gradient, all parts of a rigid particle of extension *L* (defined by copepod body length or the tips of the antenna) cannot travel with the same velocity as the fluid. If we assume that the midpoint of the copepod moves (and accelerates) with the fluid, there is a velocity difference between the midpoint and the front (or rear) end of the copepod. This velocity difference, Δw_2 , can be estimated as $\Delta w_2 = 0.5 \cdot L \cdot \partial v / \partial r$, and the strength of the signal is therefore directly proportional to the velocity gradient. Which of these 2 processes, Δw_1 or Δw_2 , dominates? We may estimate this by examining their ratio: $\Delta w_1 / \Delta w_2 = w_s \cdot v / (0.5 \cdot L \cdot a_g)$. By noting that, for the copepods considered here, the sinking velocity w_s is ~0.1 cm s⁻¹ (e.g. Tiselius & Jonsson 1990), *L* ~0.1 cm and a_g ~1000 cm s⁻², it follows that $\Delta w_1 / \Delta w_2 = v / 500$. In other words, Δw_2 is larger than Δw_1 at all fluid velocities below 500 cm s⁻¹. We can therefore conclude that the signal perceived by the copepod is directly proportional to the velocity gradient, as assumed in the model.

Our interpretation of the pipette experiments also assumes that the artificial flow field is characterised solely by along-streamline velocity gradients. However, due to the presence of a solid body in the flow (the pipette), the flow will be distorted, particularly along the sides of the pipette. Fields & Yen (1996,

1997), using experiments similar to those presented here, observed more escapes on the sides of the pipette than in front of it, and argued that the copepods respond to 'shear' rather than to the along-streamline velocity gradients. However, as noted above, the graphical presentation of the escape events folded onto the x-z plane under-represents escapes that take place in front of the pipette. Taking this into account, the escape positions observed by Fields & Yen (1996, 1997) are actually evenly distributed around the pipette mouth. Furthermore, the magnitude and spatial distribution of 'shear', as defined and estimated by Fields & Yen (velocity gradient perpendicular to the vertical direction estimated from video recordings of particle displacements), strongly depend on the orientation of the coordinate system to which the observations refer, as well as on the spatial separation distance used to estimate velocity gradients.

Our model must, however, be interpreted with caution since it is based on certain further assumptions, which may not be fully warranted: (1) the predator is spherical; (2) the calculated flow field refers to constant predator approach speed, while in fact the fish decelerates during approach; (3) the flow is assumed to be laminar, i.e. the Reynolds number is low. In fact, the Reynolds number approaches 10 and the assumption of creeping flow may be violated to some extent. Nevertheless, using independent estimates of threshold gradients from the pipette experiments, the model provided estimates of reaction distances and capture success that were of the correct order of magnitude.

Predator foraging modes and prey sensory abilities

Our model predicts that copepod reaction distance will shorten with decreasing approach velocity of the fish, but that, below a certain approach speed (at the intercept of the copepod's threshold isoline with the x-axis, Fig. 2), the copepod will not perceive the fish at all. This hyperbolic relationship between predator speed and copepod reaction distance thus conforms better with reality than the linear relationship depicted in Fig. 7, which would predict copepods reacting to a perfectly still stickleback at a distance of ~0.2 cm. This implies that, when entering the perceptive zone of the copepod (~0.5 cm with *Eurytemora affinis*), the fish needs to keep its speed below ca 0.5 cm s⁻¹, to be able to get within a strike distance (~0.1 cm) without inducing an escape. On the other hand, the model also predicts the copepod reaction distance to increase with the approach velocity of the fish. From the point of view of the predator this means that it can approach faster when it is farther away from the prey. Approaching at a constant low speed would be 'too cautious',

since it would give more time for the prey to move and, in the case of schooling fish, would provide an opportunity for the other fish to snatch the prey. An optimal strategy for sticklebacks is therefore to approach at a declining speed that, at each distance, is just below the speed that elicits an escape in the copepod. The sticklebacks indeed seemed to use this strategy: they started the approach at a high initial speed, decelerated, and used a final approach speed that was close to the maximum allowable within the copepod perceptive zone. There was a lot of variation in the fine-tuning of this strategy, however, which gave the copepods a chance to detect the predator and evade.

In contrast, the model provided an inadequate description of the *Neomysis integer*-copepod interaction: the reaction distance of either *Eurytemora affinis* or *Temora longicornis* was not correlated with mysid approach speed (cf. Fig. 7). This may be due to the fact that a mysid swims with its 4 antenna spread to form a wide sensory apparatus, and propels itself forward with its thoracic appendages. This morphology coupled with the swimming mode probably produces a strong vibration that the mechanosensing prey are able to detect, but which is difficult to model. This was supported by the long reaction distance of *E. affinis* in response to mysids. It is possible that the hydrodynamic signal generated by a mysid is not so much related to the mysid swimming speed, but to some other factor, such as the appendage beat frequency.

We recognise that a 1 l aquarium filled with filtered seawater hardly represents a natural environment for any of the experimental species. The initial prey concentrations were higher than normally occur in the study area (cf. Viitasalo 1992, Viitasalo et al. 1995). On the other hand, many copepod species show swarming behaviour, with densities reaching 500 to 2000 ind. l⁻¹ (Hamner & Carleton 1979, Ueda et al. 1983), which suggests that predators may sometimes encounter our experimental prey densities (up to 200 ind. l⁻¹) in the field. Another problem of our experimental set-up was the small size of the aquarium, which was dictated by the filming equipment. Behaviour of copepods, mysids and fish may be disturbed close to the aquarium walls, and we therefore disregarded all interactions that took place <1 cm from the walls. The sufficiency of the remaining ~8 cm wide free space depends on the spatial dimensions of escapes and attacks. According to our measurements, copepods almost never escaped for longer than 2 cm; sticklebacks detected prey from an average distance of ~2 cm, and attacked from ~0.1 cm from the prey. Total attack duration was ~0.06 s, which means that the fish darted forward 0.2 to 0.4 cm during the attacks (with average attack speeds of ~4 to 6 cm s⁻¹; cf. Table 2). Neither the copepods nor the sticklebacks were seen to hit aquarium walls during

the filming. We therefore believe that the escape behaviour of copepods and the attack behaviour of sticklebacks were not much different from those in the field. In contrast, aquarium walls apparently disturbed *Neomysis integer*; they were occasionally seen to stumble against the walls while cruising. Darkness may also have been a sub-optimal feeding condition for *N. integer*. Higher feeding rates in well-lit conditions compared to darkness have previously been observed in *Mysis relicta* (Ramcharan & Sprules 1986). On the other hand, our observations agree with other studies which have shown that *N. integer* is not an efficient feeder of adult copepods (Aaser et al. 1995, Uitto et al. 1995, A. Uitto pers. comm.).

The predation risk of the copepods studied appeared to depend more on their mechanosensory capabilities prior to attack than on the escaping performance during attack. From both predator and pipette experiments it became obvious that *Eurytemora affinis* is more sensitive to predator-generated flows than *Temora longicornis*. The 4 times higher velocity gradient threshold estimated for *T. longicornis* explains their poor escape success with sticklebacks. This difference between the sensitivities of the 2 copepod species may be a consequence of their different feeding strategies. Both species are omnivorous (Schnack 1982, Yule & Crisp 1983, Revis et al. 1991, Kleppel 1993, van Duren & Videler 1995), but observations on their feeding behaviour suggest that *T. longicornis* is relatively more confined to stationary suspension feeding than *E. affinis* (Berk et al. 1977, Tiselius & Jonsson 1990). *E. affinis* may therefore possess more sensitive hydrodynamic sensors, which enable this species to detect approaching predators from a longer distance. On the other hand, it has been shown that visual predators (Baltic herring) actively select ovigerous *E. affinis* as food (Sandström 1980, Flinkman et al. 1992). This suggests that there is a strong selection pressure towards evolving efficient escape responses in *E. affinis* females.

Conclusion

Our study confirmed that there are important differences between escape capabilities of copepod species, and that the swimming mode and the approaching skill of predators are important for their foraging success. This was highlighted by the low capture rates of sticklebacks that approached their prey too fast, and by the poor feeding success of the 'noisily' swimming mysids. We do not know if the predators showed a true preference towards either of the prey species, but we conclude that the lower escape capability of *Temora longicornis* will (in the case of a non-selective preda-

tor) result in 'apparent prey selection' towards this copepod species. The good match between the model and experimental observations was also encouraging. By using 'Occam's razor', we suggest that it is the simplest of the possible hydrodynamic cues, i.e. the velocity gradient, that elicits the escape response in copepods. This implies that, by ranking the escape performance of various zooplankton species by simple artificial flow experiments, we can predict their vulnerabilities to predation by small fish. If we compare these results with stomach content analyses of predators, we can assess which prey species are truly selected, and which are common feed just because of their poor escape capabilities. In contrast, our hydrodynamic model did not provide an adequate description of the interaction between copepods and *Neomysis integer*, and the hydrodynamic background of mysid foraging remains to be solved.

Acknowledgements. This study was financed by the Academy of Finland, the Walter and Andrée de Nottbeck Foundation and Danish Institute for Fisheries Research. T.K. was supported by a grant, #9502/63, from the Danish Natural Sciences Research Council. The experiments were conducted at Tvärminne Zoological Station, University of Helsinki. Peter Tiselius and Magnus Lindström kindly provided some of the filming equipment. We thank Brian MacKenzie and Ilppo Vuorinen for thoughtful comments on the manuscript.

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